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Reassessment of *Trilophodon connexus* Hopwood, 1935 and attributing it to the Choerolophodontidae

LI Chun-Xiao^{1,2} CHEN Jin² WANG Shi-Qi^{2*}

(1 University of Chinese Academy of Sciences Beijing 100049)

(2 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044)

* Corresponding author: wangshiqi@ivpp.ac.cn

Abstract *Trilophodon connexus* Hopwood, 1935 has long been considered a typical species of *Gomphotherium* in China. However, due to the unknown state of the mandibular symphysis and tusks, there is no definite evidence to assign “*T. connexus*” to *Gomphotherium*. Here we describe and reevaluate a hemimandible from the Halamagai Formation, Ulungur region, northern Junggar Basin, which was previously identified as *Gomphotherium* cf. *G. shensiensis*. The mandibular symphysis is deeply troughed and lacks mandibular tusks; therefore, it undoubtedly belongs to the Choerolophodontidae. Further comparison revealed that the cheek tooth morphology is identical to that of the type specimen of *Trilophodon connexus*. The characteristic features include high bunodonty, elongation of the m3 with four lophids, an only weakly chevroned lophid 2, enlargement of the posterior pretrite central conule 2, unfused state of the pretrite mesoconelet 2 (if present) and anterior pretrite central conule 2, as well as the absence of ptychodonty, choerodonty, and cementodonty. Therefore, *T. connexus* Hopwood, 1935 is a choerolophodontid rather than a species of *Gomphotherium*. Based on the above features, we provisionally refer to it as “*Choerolophodon*” *connexus*. “*Choerolophodon*” *connexus* is characterized by the following features: weak or absent ptychodonty, choerodonty, and loph chevron (which were all strong in the typical species of *Choerolophodon*), as well as multiplication of the lophids in the m3, which were similar to that of the North American *Gnathabelodon*. Therefore, *Gnathabelodon* might represent a distinct lineage within the Choerolophodontidae, and may be derived from the East Asian “*Choerolophodon*” *connexus*.

Key words Miocene, *Gomphotherium*, *Gnathabelodon*, *Choerolophodon*, proboscidean

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In several monographs on Chinese fossil proboscideans or mastodonts (Hopwood, 1935; Chow and Chang, 1974; Tobien et al., 1986), *Trilophodon connexus* Hopwood, 1935 (= *Gomphotherium connexum* (Hopwood, 1935)), is always the first introduced taxon.

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Therefore, this species was given particular attention by paleontologists working on Chinese proboscideans, and has long been regarded as a representative species of *Gomphotherium* in China, as this genus was considered the “core” group in mastodonts’ evolution (Tobien, 1973; Tassy, 1985). The type locality is Diaogou, Xining Basin, Qinghai Province, estimating ~16 Ma (Li et al., 2018). The hypodigm includes a left hemimandible bearing the m₂ and m₃ (holotype), a left M₃, and several jaw fragments and isolated cheek teeth. However, in the current view, the lack of diagnostic mandibular symphysis and mandibular tusks makes it problematic to attribute “*T. connexus*” to *Gomphotherium*. Aside from several broken mandibles and cheek teeth reported by Qiu et al. (1981), no further material from the type locality has been described.

Chen (1988) reported abundant fossil proboscideans from the Ulungur Region, northern Jungar Basin. She described two species of *Gomphotherium*, *Gomphotherium* cf. *G. shensiensis*, and *Gomphotherium* sp. Wang et al. (2015) reviewed this material. They assigned both of these two species to *G. connexum*; however, they did not suspect that “*G. connexus*” indeed belongs to *Gomphotherium*. Li et al. (2019) first reported *Choerolophodon* sp. from the Ulungur region based on several newly discovered, but rather fragmentary isolated cheek teeth. They also mentioned a mandible photographed by Chen (1988:pl.2, fig. 1, No. IVPP V8567), which she attributed to *G. cf. G. shensiensis*, and considered it as belonging to *Choerolophodon*. Indeed, this mandible possessed a long trough-like mandibular symphysis and lacks mandibular tusks, which are features that clearly diagnose the Choerolophodontidae. However, prior to 2021, none of us knew where this mandible (V8567) was deposited and the original photo is not clear enough to show the details of the morphology of the cheek teeth.

In late 2021, the second author of this paper unexpectedly discovered a long-jawed proboscidean mandible in the basement storage of the IVPP when she was performing her routine work. Although the distal symphysis was broken, it is absolutely the original specimen of IVPP V8567, which Chen (1988) had photographed. This mandible no doubt belongs to the Choerolophodontidae. Further comparison of the cheek teeth reveals that V8567 manifests almost identical characters to that of the teeth from the type hemimandibles of “*Gomphotherium connexum* (Hopwood, 1935)”, as well as to the characters of other lower cheek teeth assigned to “*Gomphotherium connexum*” from the Ulungur region. This result led us to carry out the following study: revising *Trilophodon connexus* Hopwood, 1935 and correctly transferring it to the Choerolophodontidae.

1 Material and methods

1.1 Abbreviations

Synonymy abbreviations used in this work follow Matthews (1973): *, the work validates the species; •, the authors agree on the identification at species level (maybe not at generic level); v, the authors have seen the original material of the reference; ?, the allocation of the

reference is subject to some doubt; non, the reference actually does not belong to the species under discussion; par, the reference applies only in part to the species under discussion; no sign, the authors were unable to check the validity of the reference.

Institutional abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; FHSU, Fort Hays State University's Sternberg Museum of Natural History, Hays, Kansas, U.S.A.; PMU, Palaeontological Museum, Uppsala, Sweden.

1.2 Materials, terminology, and measurements

The material described in the present work is housed in the IVPP. The comparative material is housed in the IVPP, PMU, and FHSU.

The terminology of the occlusal structure of gomphotheriid molars and mandible follows Wang et al. (2020) (Fig. 1A). Specifically, we used the terms pretrite central conule and pretrite crescentoid for different crown elements, which Osborn (1936) had previously dealt with (he used conule or serration for pretrite central conule and spur or crest for crescentoid, see Osborn, 1936:393). A pretrite crescentoid (green color) is a thick or thin enamel projection that originates from the mesial or distal side of the pretrite main cusp(id) and runs to the base of the loph(id)s (Fig. 1A, green color). The proximal end of a crescentoid merges closely with the

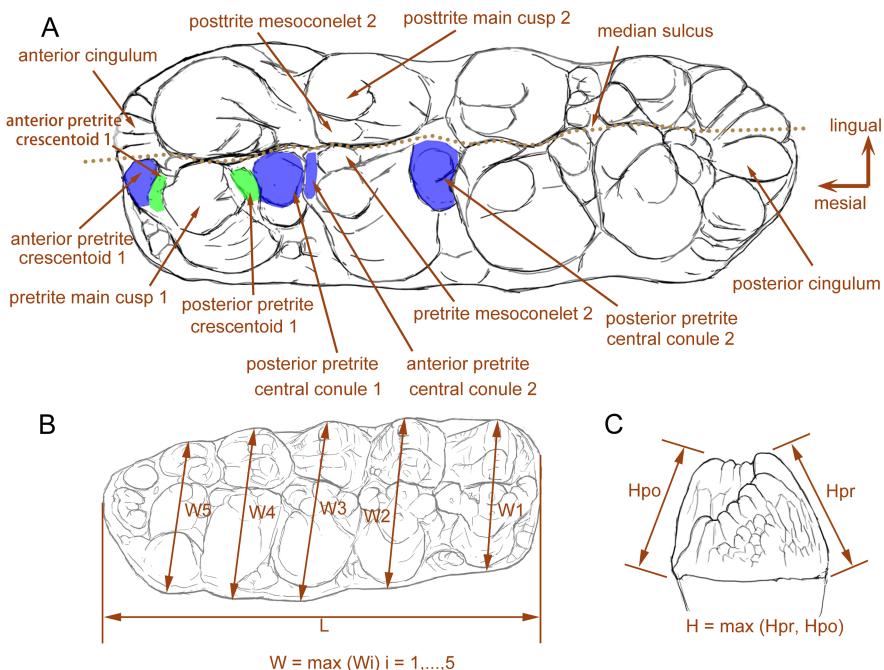


Fig. 1 Terminology and measurements of gomphothere molars

A. left m3 of “*Choerolophodon*” *connexus*, denoting the terminology of tooth crown; green color, pretrite crescentoids; blue color, pretrite central conules; B. molar crown measurements; C. molar height measurements. Abbreviations: L. length; H. height; Hpo. height of the posttrite side; Hpr. height of the pretrite side; W. width; W1, 2, ..., 5. width of the 1st, 2nd, ..., 5th loph(id)

attached main cusp(id) without a sulcus between them. Whereas a pretrite central conule (blue color) is a round bulbous cone (Fig. 1A, blue color) or subdivided enamel cones that are either arranged in a line or serrated. It should be noted that the boundary between the crescentoid and central conule might be vague after moderate or deep wear. Pretrite central conules rise directly from the base of the interloph(id) or cingulum(id) with a sulcus that clearly separates the adjacent loph(id).

Cheek tooth measurement protocol follows Tassy (2014) (Fig. 1B, C).

2 Systematics

Order Proboscidea Illiger, 1811

Family Choerolophodontidae Gaziry, 1976

Genus *Choerolophodon* Schlesinger, 1917

“*Choerolophodon*” *connexus* (Hopwood, 1935)

(Figs. 2, 3; Tables 1, 2)

*v *Trilophodon connexus* Hopwood, 1935, p. 14–19, pl. 5, figs. 1, 2

*v *Trilophodon connexus* Hopwood Osborn, 1936, p. 702, fig. 662

v non *Gomphotherium* cf. *G. connexus* (Hopwood) Zhai, 1961, p. 3, pl. 1, fig. 2

*v *Gomphotherium connexus* (Hopwood) Chow and Chang, 1974, p. 21, 22, fig. 19

• *Gomphotherium connexus* (Hopwood) Qiu et al., 1981, p. 164, 172, pl. 1, fig. 9

• *Gomphotherium connexum* (Hopwood) Tobien et al., 1986, p. 127–131, figs. 2–6

*v par *Gomphotherium* cf. *G. shensiensis* (Chang and Zhai) Chen, 1988, p. 265–268, 274–275, pl. 1, figs. 1–3, pl. 2, figs. 1–3

*v *Gomphotherium* sp. Chen, 1988, p. 268, 269, 275, pl. 3, figs. 1, 2

*v par *Gomphotherium connexum* (Hopwood) Wang et al., 2015, p. 1075–1080, figs. 2a–g, 3a–i

*v *Choerolophodon* sp. Li et al., 2019, p. 5, 6, fig. 4A–F

Diagnosis cranium and upper tusk unknown; mandibular symphysis greatly elongated, deeply concave (trough-like), and moderately ventrally bent; mandibular tusk absent; cheek teeth highly bunodont with very inflated conelets; both pretrite and posttrite mesoconelet 2 on both upper and lower molars reduced or even absent; loph/lophid 2 not, or at most weakly, chevroned; upper molars possessing a well-developed posterior pretrite central conule 2, which is usually larger than anterior pretrite central conules 2, and tends to be subdivided into two conules; posterior posttrite central conules 2 of upper molars also weakly developed; lower molars possessing a very large posterior pretrite central conule 2; m3, and even M3, showing a tendency of elongation; P3/p3 and P4/p4 present; ptychodonty and choerodonty almost absent; cementodonty weak.

Differential diagnosis differing from the derived species of the Choerolophodontidae, i.e., *Choerolophodon pentelici*, *C. anatolicus*, *C. corrugatus*, and *C. ngorora* in the weak development or absence of ptychodonty, choerodonty, and cementodonty, in the presence of

premolars, in the not chevroned loph/lophid 2; differing from *Afrochoerodon kisumuensis*, *A. zaltenensis*, “*Choerolophodon*” *chioticus*, and “*C.*” *guangheensis*, in the not chevroned loph/lophid 2, and lacking the tendency of fusion of pretrite mesoconelet 2 and anterior central conule 2; differing from *Gnathabelodon thorpei* and *Gn. buckneri* in the larger posterior pretrite central conule 2 in both upper and lower molars; differing from all species of the Choerolophodontidae in the weak development or absence of pretrite and posttrite mesoconelet 2 on both upper and lower molars.

Type specimens holotype, PMU-M 3469, a left hemimandible with m2 and m3, lacking mandibular symphysis. A cast, IVPP RV35015, were housed in IVPP.

Type locality and horizon Diaogou, Xining City, Qinghai Province. The Diaogou locality situates at the base of the Miocene Guanjiashan Formation, the age was estimated ~16 Ma (Li et al., 2018).

Referred specimens from Diaogou PMU-M 3045 (IVPP RV35D49, a cast), a left M3; PMU-M 3047, a left P4; PMU-M 3049, a left hemimandibles carrying a dentition of p3, dp4, and m1; PMU-M 3046, a right p4; PMU-M 3048, a left m2; IVPP V6019.1, left hemimandible with m2 and m3.

Referred specimens from Ulungur region, northern Junggar Basin IVPP V8567, a left hemimandible with mandibular symphysis, m2 and m3; V8573, V8574, and V8576, three left M3; V8572, a right M3; V8569, a left dp4; V8575 and V18701, two left m3, V31357, a right m2, V25051, maxillary fragments with M2 and partial M3, V25057, mesial two lophs of M2 or M3, V25058, a fragmented right m3. Except the last one, which is from the very base of Kekemaideng Formation (~14.5 Ma), other specimens are from Halamagai Formation (~16.9–15 Ma) (Wang et al., 2022).

Descriptions Most of the above specimens have been described at least once, in some cases even multi-times (e.g., the holotype) in the previous works (Hopwood, 1935; Chow and Chang, 1974; Chen, 1988, 2021; Tobien et al., 1986; Wang et al., 2015; Li et al., 2019). Here we describe only IVPP V8567 (the critical material which had not been carefully described before) and V31357 (newly discovered).

IVPP V8567 is a left hemimandible with symphysis, bearing the m2 and m3 (Fig. 2A, B, G, K, O, Q), which had previously been photographed by Chen (1988). In the original photo, the symphysis is complete (Fig. 2A), but in the current state, the distal end of the symphysis, especially the left side, is missing (Fig. 2B). The symphysis was broken into two parts at about one third of the proximal, and the two parts could not be completely matched due to the extra loss of the adjacent bone. In dorsal view, the symphysis is very long (longer than the corpus). It is deep and trough-like, and the bony wall is very thin, which is evidently not holding any tusk (Fig. 2Q). The symphysis is slightly transversely expanded distally, and as seen from the original photo, two transversely elongated rough areas are present, with each one aside the mid-axis of the distal end, which possibly represents the remnant of the opening of the tusk alveolus (Fig. 2A). In lateral view, the symphysis is moderately ventrally inflected (close to

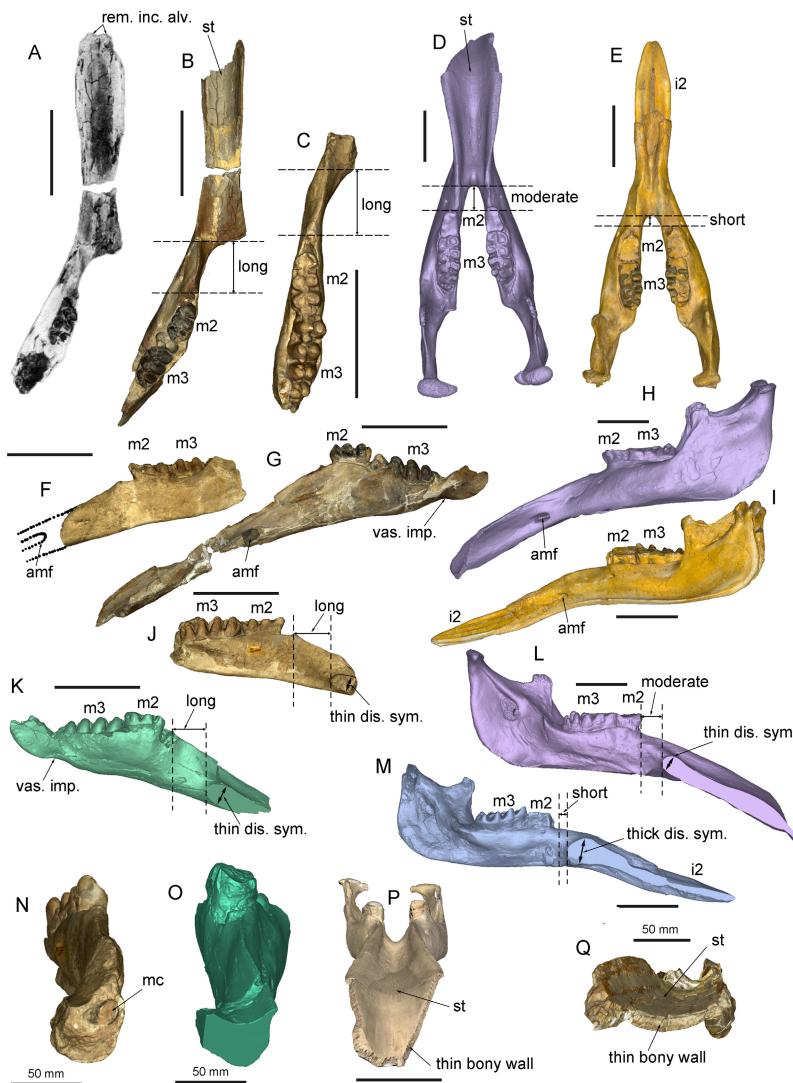


Fig. 2 Mandible of “*Choerolophodon*” *connexus* and *Gnathabelodon*, in comparison with *Gomphotherium*. A, B, G, K, O, Q. “*Choerolophodon*” *connexus*, IVPP V8567, from Halamagai Formation, Ulungur region: A. the original photo in Chen (1988:pl. 2, fig. 1); C, F, J, N. “C.” *connexus*, IVPP RV35015 (cast of the type specimen, PMU-M 3469), from Diaogou, Guanjiashan Formation (formerly Xianshuilie Formation), Xining Basin; D, H, L, P. *Gnathabelodon thorpei*, FHSU VP18, type specimen, from Ogallala, Kansas, U.S.A., late Clarendonian; note that the distal end of the mandibular symphysis is repaired by plaster; E, I, M. *Gomphotherium tassyi*, IVPP V22781, from Heijiagou, upper part of Zhangenbao Formation, Zhongning Region

A–E. in dorsal view, showing the deep symphyseal groove and long or moderate distance between the distal end of symphysis and the anterior end of the cheek tooth row; F–I. in left lateral view, showing the tube-like anterior mental foramen; J–M. in right medial view, showing long or moderate distance between the distal end of symphysis and the anterior end of the cheek tooth row, as well as the thin distal end of symphysis; note that K–M were cut along the middle sagittal plane from 3D models; N–Q. in distal view, showing the large mandibular channel (N), and thin bony wall of distal symphysis (P, Q); note that O (“C.” *connexus*, IVPP V8567) was cut from the same position as N (type), which has been broken. Abbreviations: amf. anterior mental foramen; i2. the second lower incisor (mandibular tusk); m2, 3. the second, third lower molar; mc. mandibular channel; rem. inc. alv. remnant of incisor alveolus; st. symphyseal trough; thick/thin dis. sym. thick/thin distal symphysis; vas. imp. vascular impression for facial artery and vein. Scale bars without notations equal to 20 cm

Table 1 Cheek teeth measurements of “*Choerolophodon*” *connexus* and *Gnathabelodon thorpei* (mm)

no.	species	locality /region	locus	L	W	W1	W2	W3	W4	Hpo	W/L
*RV35D49	“C.” <i>connexus</i>	Diagou	I. M3	120.01	62.08	62.08	60.00	57.11		41.26 ⁽²⁾	0.52
*V8572	“C.” <i>connexus</i>	Ulungur	r. M3	186.93	83.78	83.78	76.75	72.1	63.36	51.28 ⁽²⁾	0.45
*V8573	“C.” <i>connexus</i>	Ulungur	I. M3	170.72	82.74	82.74	77.1	72.31	50.86	50.41 ⁽³⁾	0.48
*V8576	“C.” <i>connexus</i>	Ulungur	I. M3	176.15	74.93	74.93	71.58	67.61	57.56	50.70 ⁽³⁾	0.43
*V8574	“C.” <i>connexus</i>	Ulungur	I. M3	—	—	—	—	67.24	59.95	57.15 ⁽³⁾	—
VP18	<i>Gn. thorpei</i>	Ogallah	r. M3	196.35	105.7	97.62	105.7	104.27	81.81	58.41+ ⁽³⁾	0.54
*V8569	“C.” <i>connexus</i>	Ulungur	I. dp4	71.83	37.82	—	—	37.82		33.12 ⁽²⁾	0.53
V31357	“C.” <i>connexus</i>	Ulungur	r. m2	109.59	56.62	45.59	54.96	56.62		40.8+ ⁽³⁾	0.52
*V8567	“C.” <i>connexus</i>	Ulungur	I. m2	—	56.93	—	52.02	56.93		33.32+ ⁽³⁾	—
*RV35015	“C.” <i>connexus</i>	Diagou	I. m2	103.49	45.13	38.97	45.13	50.23			0.44
V8567	“C.” <i>connexus</i>	Ulungur	I. m3	158.44	65.19	—	63.71	65.19	53.66	45.62+ ⁽²⁾	0.41
*RV35015	“C.” <i>connexus</i>	Diagou	I. m3	148.52	51.45	50.68	51.45	—	—	46.72+ ⁽²⁾	0.35
*V18701	“C.” <i>connexus</i>	Ulungur	I. m3	191.09	68.1	68.1	65.22	67.31	65.05	54.14 ⁽²⁾	0.36
*V8571	“C.” <i>connexus</i>	Ulungur	r. m3	172.02	76.04	68.37	76.04	67.32	52.38	58.51 ⁽²⁾	0.44
*V8575	“C.” <i>connexus</i>	Ulungur	I. m3	169.99	64.27	57.31	64.27	58.47	51.31	58.03 ⁽¹⁾	0.38
VP18	<i>Gn. thorpei</i>	Ogallah	I. m3	209.85	91.15	80.65	89.44	91.15	78.91	66.37+ ⁽³⁾	0.43
VP18	<i>Gn. thorpei</i>	Ogallah	r. m3	198.82	91.53	79.96	90.03	91.53	74.24	67.45+ ⁽³⁾	0.46

Notes: *, data after Wang et al. (2015); Hpo: height of the posttrite side [numbers in brackets indicate the loph(id) from which the measurement was taken]; L: length; W: maximal width; W1, 2, 3, and 4: width at the first, second, third, and fourth loph(id).

Table 2 mandibular measurements of “*Choerolophodon*” *connexus*, *Gnathabelodon thorpei* and *Gomphotherium tassyi* (mm)

Mandibular measurements	<i>Gnathabelodon</i>	<i>Gomphotherium</i>	“ <i>Choerolophodon</i> ”	
	<i>thorpei</i>	<i>tassyi</i>	<i>connexus</i>	
	FHSU	IVPP	IVPP	IVPP
maximal length	1490.8	1160.8	760.1	483.5+
symphyseal length	587.4+	584.0	403.5+	—
maximal width	596.1	492.7	—	—
posterior symphyseal width	258.4	185.0	158.6	161.4
anterior symphyseal width	—	114.6	—	—
maximum symphyseal width	221.9	186.3	—	—
minimum symphyseal width	176.5	108.1	83.4	—
maximum width of the rostral trough	214.8	—	—	—
minimum width of rostral trough	168.7	—	80.2	50.3
internal width between anterior alveoli (or grinding teeth if the alveoli are resorbed)	89.4	76.4	—	60.2
maximum height of horizontal ramus (measurement taken perpendicular to the ventral border of the ramus)	478.1	388.7	—	94.5
height of horizontal ramus taken at the root of the ascending branch (measurement as above)	210.5	175.7	—	76.5
rostral height taken at the symphyseal border (measurement taken perpendicular to the ventral border of the symphyseal rostrum)	207.5	120.5	98.5	61.2
rostral height taken at the tip of rostrum (measurement as above)	169.0	98.4	—	47.0
maximum depth of the ascending ramus	305.4	146.8	—	172.8
depth between gonion and the coronoid process	310.8	172.4	—	191.1
mid-alveolar length taken on the buccal side between the anterior alveolus and the root of the ascending ramus	335.8	243.0	245.4	236.0
rostral height taken at the tip of rostrum (measurement as above)	169.0	98.4	—	47.0
maximum depth of the ascending ramus	305.4	146.8	—	172.8
depth between gonion and the coronoid process	310.8	172.4	—	191.1
mid-alveolar length taken on the buccal side between the anterior alveolus and the root of the ascending ramus	335.8	243.0	245.4	236.0

that of *Gnathabelodon thorpei*) (Fig. 2G), and the anterior mental foramen is very large and tube-like (Fig. 2G), indicating the development of a keratinous structure from the integument of the distal symphysis. In medial view, the proximal end of the symphysis is relatively distant from the cheek tooth row; dorso-ventrally, it is very thin compared to that of the other longirostrine taxa that possess lower tusks (Fig. 2K). The mandibular corpus is strong, and its height at the rostral end is relatively large. However, a large amount of bony structure around the m3 is just missing. Most of the ramus is broken, and a deep vascular impression ventral to the ramus for the facial artery and vein is very pronounced (Fig. 2G, K).

The m2 is deeply worn (Fig. 3A). It is rectangular with three lophids. The lophid 1 is only partially preserved. The dentine of the pretrite and posttrite half lophids 2 are connected to each other due to heavy wear. The lophid 3 is moderately worn. The pretrite half lophid has an anterior and a posterior central conule, which are both large, and the latter is fused with a strong conule that rises directly from the buccal side of the distal cingulid. Another isolated conule also rises from the lingual side of the distal cingulid.

The m3 is erupting from the alveolus and the adjacent bones were removed (Fig. 3A). It is highly bunodont with complete four lophids and a distal cingulid. The pretrite lophid 1 has well developed anterior and posterior central conules. The former is subdivided into two conules and the latter is large, and it links to the main conelet with a strong arm (a short and thick posterior crescentoid). The posttrite half lophid has a large main conelet and a small mesoconelet. The pretrite lophid 2 has a weak anterior central conule, a weak mesoconelet, and a large posterior central conule that rises directly from the interlophid 2. The posttrite lophid 2 has a large main conelet and a very thin flaky mesoconelet. The pretrite and posttrite half

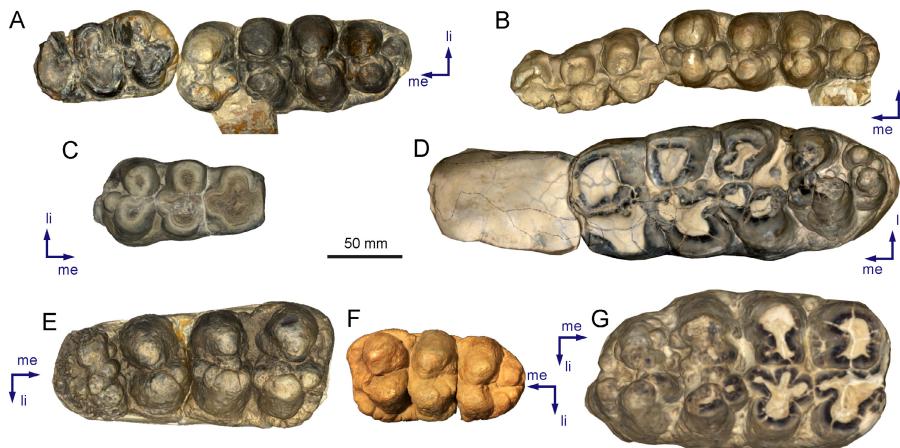


Fig. 3 Cheek teeth of “*Choerolophodon*” *connexus* and *Gnathabelodon*

- A. “*Choerolophodon*” *connexus*, left m2 and m3, IVPP V8567; B. “*C.*” *connexus*, left m2 and m3, IVPP RV35015; C. “*C.*” *connexus*, right m2, IVPP V31357, from Halamagai Formation, Ulungur region;
- D. *Gnathabelodon thorpei*, left m2 and m3, FHSU VP18, type specimen; E. “*C.*” *connexus*, right M3, IVPP V8572, from Halamagai Formation, Ulungur region; F. “*C.*” *connexus*, left M3, IVPP RV35D49 (cast of PMU-M 3045), from Diaogou, Xining Basin; G. *Gn. thorpei*, right M3, FHSU VP18

Abbreviations: li. lingual side; me. mesial side

lophids are almost not chevroned. The lophid 3 shows very similar morphology to the lophid 2, except that the anterior and posterior pretrite central conules are nearly equivalent, and the posttrite mesoconelet is slightly thicker in the lophid 3. The lophid 4 has a simple trifoliate pretrite half lophid and lacks the posttrite mesoconelet. Only a large conelet rises from the posterior cingulid. Ptychodonty and cementodonty are absent.

IVPP V31357 (Fig. 3C) is a newly discovered specimen from the Dingshanyanchi locality, Halamagai Formation. It is a deeply worn right m₂ and shows a morphology that is very similar to the type m₂ (Fig. 3B). The firstly two lophids are deeply worn, with the two half lophids connected to each other. The posterior posttrite central conules 1 and 2 are large. The lophid 3 is simple, with a large posterior posttrite central conule directly rising from the distal cingulid. The pretrite and posttrite mesoconelets are weak. A small amount of cementum is deposited in the interlophids.

3 Comparison and discussion

The primary difference between the Choerolophodontidae and other longirostrine elephantiforms is that the former possesses a through-like mandibular symphysis and lacks mandibular tusks (Tassy, 1983; Konidaris et al., 2016; Li et al., 2019). Therefore, IVPP V8567, the hemimandible from Halamagai Formation, Junggar Basin, is without a doubt a choerolophodontid. The following is concerned with the comparison of V8567 and the type mandible PMU-M 3469.

PMU-M 3469 is also a left hemimandible (Fig. 2C, F, J, N). However, it is missing the vast majority of the symphysis, except for the most proximal part. In comparing the proximal end of the mandibular symphysis with the Halamagai mandible, IVPP V8567 (Fig. 2A, B, G, K, O, Q), and with a “true” *Gomphotherium*, V22781 (Fig. 2E, I, M), it can be seen that both PMU-M 3469 (type) and V8567 have a very dorso-ventrally thin proximal extremity of the mandibular symphysis (Fig. 2J, K, thin dis. sym.) that is a relatively far distance from the cheek teeth row (Fig. 2B, C, J, K), which suggests that the mandibular symphysis is very weak and could not hold a tusk. However, in the mandible of *Gomphotherium tassyi*, which has a pair of strong mandibular tusk, the symphyseal proximal extremity is dorso-ventrally thick and close to the cheek teeth row (Fig. 2E, M, thick dis. sym.). Tobien et al. (1986) mentioned that “an alveolus of incisor” is present in the type cast, and they even argued that the tusks have been weakened in “*G. connexum*”. However, we did not agree with this because an alveolus cannot be inserted so deeply (as to reach the very base of the proximal end of symphysis), and it is not positioned so dorsally and laterally (tusk alveolus should be very close to the mid-axis). What they mentioned is in fact the mandibular channel that links to the anterior mental foramen (Fig. 2N, mc). In choerolophodontids, the anterior mental foramen (and the following mandibular channel) is very thick and tube-like.

The cheek teeth of the two specimens are in a very similar ontogenetic stage, which

facilitates the comparison (Fig. 3A, B). It is unnecessary to compare the deeply worn m₂, and only the diagnostic characters of the m₃ will be discussed. The m₃s of both specimens are highly bunodont. They are relatively narrow, and they are composed of four lophids and a distal cingulid. The lophid 2 (the most characterized part of a cheek tooth) of both m₃s are almost not chevroned and only show a slight mesial shifting of the pretrite mesoconelet, which is rather weak. The posttrite mesoconelet is almost absent in the m₃ of both specimens. The posterior pretrite central conule 2 rises directly from the interlophid without a link (posterior crescentoid) to the main conelet. The anterior pretrite central conule 2 is small. In the lophid 1 of both m₃s, the posterior pretrite central conule is very large, links to the main conelet with a thick posterior crescentoid, and the anterior pretrite central conule is subdivided into two isolated conules that link to the mesial cingulid. The pretrite mesoconelet is moderately developed and the posttrite mesoconelet is either weak (Halamagai m₃) or absent (type m₃). Finally, choerodonty, ptychodonty, and cementodonty are absent in both m₃s, and they are even similar in size (Table 1). Therefore, both m₃s are identical in critical characters, and these characters are also the diagnostic characters of the species “*connexus*”. Finally, the Halamagai mandible seems to be slightly more derived than the type mandible in the more ventrally inflected symphysis, and in the earlier eruption of the m₂. Except for these minor differences, these two mandibles can be attributed into the same species “*connexus*” but belong to the Choerolophodontidae rather than to *Gomphotherium*.

Additionally, Wang et al. (2015) also provided strong evidence that the upper molars from the type locality and from the Halamagai Formation belong to the same species, “*connexus*”, and we will not repeat this comparison (Fig. 3E, F). Hereby we transfer them to the Choerolophodontidae altogether. Moreover, we also attribute *Choerolophodon* sp. from the Ulungur region reported by Li et al. (2019) to the species “*connexus*”.

It should be noted that the hypodigm of *Trilophodon connexus* Hopwood, 1935 includes several premolars, i.e., PMU-M 3047 (a P₄), and PMU-M 3049 (left juvenile hemimandibles bearing a p₃) (Tobien et al., 1986:figs. 3, 4). Although Tassy (1983) previously mentioned that premolars are yet unknown in the Choerolophodontidae, it is no surprise that premolars were still developed in a relatively primitive evolutionary stage of this family. Wang and Deng (2011) reported P₄s in *Choerolophodon guangheensis*, and Wang et al. (2023) found a P₃ in *C. guangheensis*. Here, even a p₃ was found in “*connexus*” (a p₄ should be also present) despite the fact that this premolar is very small and very easily shed.

The next step is to determine to which genus *Trilophodon connexus* Hopwood, 1935 should be attributed within the Choerolophodontidae. Unfortunately, a common agreement on the generic taxonomy of the Choerolophodontidae has not yet been reached. Before 2001, *Choerolophodon* was the only included genus. Pickford (2001) established *Afrochoerodon* based on *Choerolophodon kisumensis* (Macinnes, 1942), *C. zaltanensis* Gaziry, 1987, *C. ngorora* (Maglio, 1974), and *C. chioticus* Tobien, 1980. In the recent studies, *Afrochoerodon* was considered the paraphyletic ancestral group of *Choerolophodon* (Shoshani and Tassy, 2005),

and Konidaris et al. (2016) reattributed all the species into *Choerolophodon*. However, in some of the other existing literature (Sanders and Miller, 2002; Sanders et al., 2010), *Afrochoerodon kisumensis* was still used, and *C. palaeindicus* was sometimes attributed to *Afrochoerodon*. Li et al. (2019) attributed North American *Gnathabelodon* to the Choerolophodontidae. In this case, which group was *Gnathabelodon* derived from remains an interesting issue.

There is no doubt that the mandible of *Gnathabelodon thorpei* (FHSU VP18) (Barbour and Sternberg, 1935) (Fig. 2D, H, L, P), as well as that of *Gn. buckneri* (Sellards, 1940), resemble all the known Early and Middle Miocene choerolophodontid mandibles, including the mandible of *Choerolophodon chioticus* and the Halamagai mandible (IVPP V8567), except the much larger size of *Gn. thorpei*. Here, we will further compare the cheek tooth morphology. The lower m3 of *Gn. thorpei* and *Gn. buckneri* possesses four lophids with a distal cingulid (Fig. 3D). The pretrite half lophid 2 is situated at the normal position seen in most gomphotheres, and the pretrite mesoconelet 2 is not fused with the corresponding anterior central conule. These characters were all seen in “*connexus*”. However, in some derived species of *Choerolophodon*, including the type species *Choerolophodon pentelici*, *C. ngorora*, and *Afrochoerodon kisumensis*, the pretrite half lophid 2 of the lower molars shifts to a very buccal position, and the pretrite mesoconelet 2 and anterior central conule 2 are fused.

The upper M3 of *Gn. thorpei* possesses four lophids (Fig. 3G). The loph 2 is almost not chevroned, the pretrite mesoconelet 2 and anterior central conule 2 are clearly individualized (without any tendency for fusion), and the posterior pretrite central conule 2 is large (a synapomorphy of *Gnathabelodon* within the Choerolophodontidae). These characters also resemble those of “*connexus*”. In *Choerolophodon pentelici*, *C. ngorora*, *C. corrugatus*, and *Afrochoerodon kisumensis*, the loph 2 is strongly chevroned, the pretrite mesoconelet 2 and anterior central conule 2 are fused, and the posterior pretrite central conule 2 is weak (possibly even absent). Furthermore, choerodonty, ptychodonty, and cementodonty are all not pronounced in the molars of *Gn. thorpei*, which is also close to what is observed in “*connexus*”. After all, loph/lophid 2 chevroning, choerodonty, ptychodonty, and cementodonty were previously considered to be the typical characters of choerolophodontids (Tassy, 1983; Konidaris et al., 2016). However, this observation may not be suitable for all choerolophodontid members. *Gnathabelodon* might represent a distinct lineage in the very initial evolution of loph/lophid 2 chevroning, choerodonty, ptychodonty, and cementodonty, but shows a tendency for the enlargement of the posterior pretrite central conule 2, as well as m3 elongation. Therefore, the morphology of “*connexus*” is closer to that of *Gnathabelodon thorpei* than to that of species of *Choerolophodon* and *Afrochoerodon*. However, before a comprehensive phylogenetic study and a complete revision of all choerolophodontid species have been done, we provisionally assign “*connexus*” into the type genus *Choerolophodon*, with quotation marks, i.e., “*Choerolophodon*” *connexus* (Konidaris et al. (2016) also attributed all species into *Choerolophodon*). Nevertheless, “C.” *connexus* provides a missing link between the Old-World choerolophodontids with the New-World enigmatic proboscidean *Gnathabelodon*.

4 Conclusion

In the present article, we transfer *Trilophodon connexus* Hopwood, 1935 to “*Choerolophodon*” *connexus*. Lacking a comprehensive amending of the Choerolophodontidae, this attribution is somewhat provisional. However, we have identified the possible origin of North American *Gnathabelodon thorpei*, which has long been considered an enigmatic taxon. “*Trilophodon connexus* Hopwood, 1935” has been considered a representative *Gomphotherium* in China because of its highly bunodont cheek tooth morphology. The reevaluation of the mandible from the Halamagai Formation of the Ulungur region compels us to remove it from *Gomphotherium*. Our empirical studies in Chinese gomphotheres reveal that “true *Gomphotherium*” is relatively rare in China, especially for such a highly bunodont taxa. As *G. spectabilis* was synonymized with *Platybelodon grangeri* (Amebelodontidae) (Tobien et al., 1986); and *G. wimani* should be revised as *Protanancus wimani* (Amebelodontidae) (Wang, 2021; Wang et al., 2023); Furthermore, *G. connexum* is transferred to “*Choerolophodon*” *connexus* (Choerolophodontidae). It is confirmed that *Gomphotherium* from China includes the following species: *G. cooperi* from the Tongxin region (Li et al., 2022), *G. inopinatum* from Linxia Basin (Wang, 2014), *G. tassyi* from Linxia Basin and the Zhongning region (Wang et al., 2017), and *G. steinheimense* from the Ulungur region (Wu et al., 2018). Nevertheless, in the Early and Middle Miocene of China, *Gomphotherium* is relatively rare, and members of the Choerolophodontidae and Amebelodontidae are the dominant groups in gomphotheres.

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间型三棱齿象(*Trilophodon connexus* Hopwood, 1935)

属于豕棱齿象类而非嵌齿象

李春晓^{1,2} 陈 津² 王世骐²

(1 中国科学院大学 北京 100049)

(2 中国科学院古脊椎动物与古人类研究所, 中国科学院脊椎动物演化与人类起源重点实验室 北京 100044)

摘要: 间型三棱齿象(*Trilophodon connexus* Hopwood, 1935)长期以来被认为是中国嵌齿象属(*Gomphotherium*)的一个代表种。然而, 由于其下颌联合部与下门齿的形态未知, 这一归入存疑。重新研究了来自新疆准噶尔盆地北缘乌伦古河地区哈拉玛盖组的一件此前归为陕西

嵌齿象相似种(*Gomphotherium* cf. *G. shensiensis*)的下颌。该下颌联合部伸长，呈深槽状，下门齿缺失，因此确定可归入豕棱齿象科(Choerolophodontidae)。进一步将间型三棱齿象的正型标本与其相比较，两者颊齿的关键特征完全一致，包括：高度丘型化，m3伸长，具有四脊，上下颊齿第二脊“人字型”(chevron)很弱，第二脊中附锥与前中心小尖不愈合，釉质褶皱、齿谷中小锥及白垩质发育弱或缺失。因此，间型三棱齿象事实上是一种豕棱齿象类而非嵌齿象。综上所述，暂将其改定为间型“豕棱齿象” (“*Choerolophodon*” *connexus* (Hopwood, 1935))。同时，以上特征与北美的索普颌门齿象(*Gnathabelodon thorpei*)比较接近。此外，在颌门齿象属和间型“豕棱齿象”中，颊齿第二脊呈“人字型”，釉质褶皱、齿谷中小锥及白垩质发育强这些典型的豕棱齿象属(*Choerolophodon*)的特征较弱甚至缺失，但m3齿脊数变多，这表明颌门齿象属可能起源于东亚的间型“豕棱齿象”。

关键词：中新世，嵌齿象，颌门齿象，豕棱齿象，长鼻类

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